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Central Concepts and Issues of Landscape Ecology

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"... the grand challenge is to forge a conceptual and theoretical synthesis of spatial ecology, embracing in one manner or another individual responses and population dynamics, and explaining patterns in species abundance caused by complex landscapes and patterns driven by complex dynamics" (Hanski 1999:264).

1.1 Introduction

The objective of biological conservation is the long-term maintenance of populations or species or, more broadly, of the Earth's biodiversity. Many of the threats that elicit conservation concern result in one way or another from human land use. Population sizes may become precariously small when suitable habitat is lost or becomes spatially fragmented, increasing the likelihood of extinction. Changes in land cover may affect interactions between predator and prey or parasite and host populations. The spread of invasive or exotic species, disease, or disturbances such as fire may be enhanced by shifts in the distribution of natural, agricultural, or urbanized areas. The infusion of pollutants into aquatic ecosystems from terrestrial sources such as agriculture may be enhanced or reduced by the characteristics of the landscape between source and end point. Virtually all conservation issues are ultimately land-use issues.

Landscape ecology deals with the causes and consequences of the spatial composition and configuration of landscape mosaics. Because changes in land use alter landscape composition and configuration, landscape ecology and biological conservation are obviously closely linked. Both landscape ecology and conservation biology are relatively young disciplines, however, so this conceptual marriage has yet to be fully consummated. My objectives in this chapter are to provide some general background about landscapes and landscape ecology (Section 1.2), to develop the emerging concepts and principles of landscape ecology and show how they may affect the features of ecological systems that are important to conservation efforts or management (Section 1.3), to touch briefly on some issues that may affect the integration of landscape ecology into biological conservation (Section 1.4), and to offer some concluding, philosophical comments about the future role of landscape ecology in conservation (Section 1.5). Many of these points will be developed in more detail in the remainder of this volume.

1.2 General Background

1.2.1 *What Are Landscapes and What Is Landscape Ecology?*

Although there are many definitions of "landscape" in the geographical and ecological literature (as well as in various dictionaries), all are characterized by two themes: *landscapes* are composed of multiple elements (or "patches"), and the variety of these elements creates heterogeneity within an area. From a conservation perspective, a landscape contains multiple habitats, vegetation types, or land uses. There is more to it than this, however. The elements of a landscape have a particular spatial configuration, which can be portrayed as a map or (more fashionably now) as a geographic information system (GIS) image. It is the spatial relationships among landscape elements as much as their variety that make landscapes important, for these relationships can affect the interactions among the elements in a mosaic as well as what goes on within individual patches.

Agreement about the characteristics of "landscapes" generally stops here, however. It is commonplace, for example, to find references to the "landscape level" in the ecological and conservation literature. Here, the landscape is viewed as a level in an ecological hierarchy: "landscape" is more inclusive than an ecosystem, yet it is nested within a biome—it is a collection of ecosystems (e.g., Forman and Godron 1986; Noss 1991). This view pervades the use of "landscape" in resource management, in which actions at the landscape level are advocated because they encompass more variety than do actions focused on individual habitats, land-cover types, or administrative units such as reserves or parks. Others refer to the "landscape scale," by which they generally mean a spatial scale of resolution that corresponds with human perceptions of their surroundings—a scale of tens of hectares to kilometers (e.g., Forman 1995). One can find "landscape" used in both of these senses throughout this book.

This emphasis on "landscape" as a level or a scale stems in part from the everyday use of the word, which carries with it both human visualizations of landscapes as well as the human desire to order phenomena hierarchically. It also reflects the historical roots of landscape ecology as a discipline. Landscape ecology began in northern and eastern Europe through a merging of holistic ecology with human geography, land-use planning, landscape architecture, sociology, and other disciplines (Naveh and Lieberman 1994; Zonneveld 1995; Wiens 1997). From its birth, then, landscape ecology carried with it a focus on interactions of humans with their environment at broad spatial scales. Although the recent growth of landscape ecology as a discipline has incorporated closer linkages with traditional (i.e., nonhuman) ecology, the utility in management of thinking of landscapes in human terms has perpetuated and reinforced this anthropocentric perspective. After all, decisions about land management or land-use policy are made with reference to the scales of human activities and the hierarchical structure of administrative bodies.

Despite this, there are both logical and operational reasons for arguing that viewing "landscape" as a level or a scale is wrong, or at least unnecessarily restrictive. King (1997, 1999), Allen (1998), and O'Neill and King (1998) have discussed the logical arguments. Briefly, they argue that "level" in an organizational hierarchy must be defined on the basis of similarities in rate processes. Entities that belong to the same level operate at similar rates and therefore can interact with one another, whereas components with different rate structures cannot interact but can only constrain the dynamics of other levels. What is a "level" therefore depends on the scale of observation and the question the investigator asks. In a similar vein, "landscape" represents an arbitrary definition by the observer of a certain kind of object or class, whereas "scale" refers to the physical dimensions of an object or class in space and time. Specifying the class ("landscape") does not necessarily specify a scale, because the way the class is defined may differ among investigators depending on the question or perspective. References to "landscape level" or "landscape scale" therefore mix terms that are logically derived in different ways, and this can lead to imprecision in both meaning and measurement.

Operationally, by restricting consideration of landscape properties and their ecological consequences to certain levels or scales, one essentially denies the relevance of landscape structure to other levels or scales. This can lead to an unintended acceptance of the assumption that neither heterogeneity nor scale is important at those levels or scales. But heterogeneity and scale dependency can affect ecological patterns and processes at the levels of individuals, populations, or communities as well as ecosystems or biomes, and they are expressed on scales covering a few centimeters or meters as well as hectares or kilometers. It is important to realize that what makes landscapes interesting and important to ecology and conservation is not only the emphasis on broad scales or more inclusive levels of organization, but also on how the spatial configuration and dynamics of landscape mosaics influence predation, dispersal, population dynamics, nutrient distribution, or disturbance spread—indeed, virtually all ecological phenomena.

Contained within these varying views about "landscapes" are the elements of three different approaches to landscape ecology, each of which implies something different about how landscape ecology may contribute to biological conservation. One approach derives directly from the European tradition, and it considers landscape ecology as a "holistic, problem-solving approach to resource management" (Barrett and Bohlen 1991). The emphasis is on integrating many aspects of human activities with their environmental consequences—a geographically based resource-management approach.

The second approach emphasizes landscape as a level or scale; in essence, it is ecology writ large. Many of the questions are those that ecologists have traditionally addressed, but they are cast in a broader hierarchical or spatial context. This approach has clear linkages to biogeography and the developing area of macroecology (Brown 1995). It is clearly relevant to regional planning and to geographically defined conservation efforts, such as those dealing with ecoregions (e.g., Ricketts et al. 1999; Poiani et al. 2000) or with the regional distribution of biodiversity "hotspots" (e.g., Reid 1998; Flather et al. 1998).

The third approach deals more explicitly with the causes and consequences of spatial patterns in the environment, with the effects of spatial pattern on ecological processes (Turner 1989; Wiens et al. 1993; Wiens 1995). In this case, the level and scale are determined by characteristics of the organisms or ecological systems of interest and the questions asked (Wiens 1989a; Haila 1999; Mac Nally 1999). The focus of this approach is on the mechanisms by which the spatial structure of the environment influences phenomena of conservation value such as populations or biodiversity. The scales on which these mechanisms are expressed (and thus the "landscape") therefore will differ for different kinds of organisms (e.g., Wiens and Milne 1989). This approach actually embodies two somewhat different perspectives: *spatial ecology,* which considers only how spatial variation in environmental factors affects ecological systems (e.g., Tilman and Kareiva 1997), and *landscape ecology,* which also considers explicit spatial relationships and locational effects.

Without denying the value of the first two approaches to biological conservation, my emphasis in this chapter will be on the third approach, especially the landscape perspective. I emphasize this approach because I believe that it provides the best way to derive insights about how the spatial texture and configuration of landscapes can influence ecological systems and their dynamics. If most conservation issues are indeed ultimately tied to human land use, the importance of such understanding should be obvious.

1.2.2 What Features Characterize Landscapes?

Saying that a landscape approach emphasizes the causes and consequences of heterogeneity or of spatial pattern serves to reinforce the ongoing paradigm shift away from viewing ecological systems as spatially homogeneous (Pickett et al. 1992; Wiens 1995). Words like "heterogeneity" or "spatial pattern," however, are too nebulous to be of much use in characterizing what we need to know about landscapes to gauge their effects. More detail is needed.

Conceptually, the components of a landscape can be partitioned into features of *composition,* the kinds of elements or patches making up a landscape; *structure,* its physical configuration; and *process,* the flows of organisms, materials, or disturbances through the mosaic (Figure 1.1a; Chapter 3). Operationally, we usually express landscapes as maps or images, which incorporate the compositional and structural aspects of landscapes but not process or (except as a time series of maps) dynamics. To derive a map requires drawing boundaries around units so their spatial distribution can be portrayed. Geographers and cartographers have wrestled with the problems of boundary determination and map classification for decades (e.g., Küchler 1974; Bailey 1996; Monmonier 1996); here, I will only note that how these decisions are made affects not only the map, but also all of the analyses and conclusions that follow from it. If vegetation cover is classified in different ways, for example, interpretations of how a wildlife species of concern

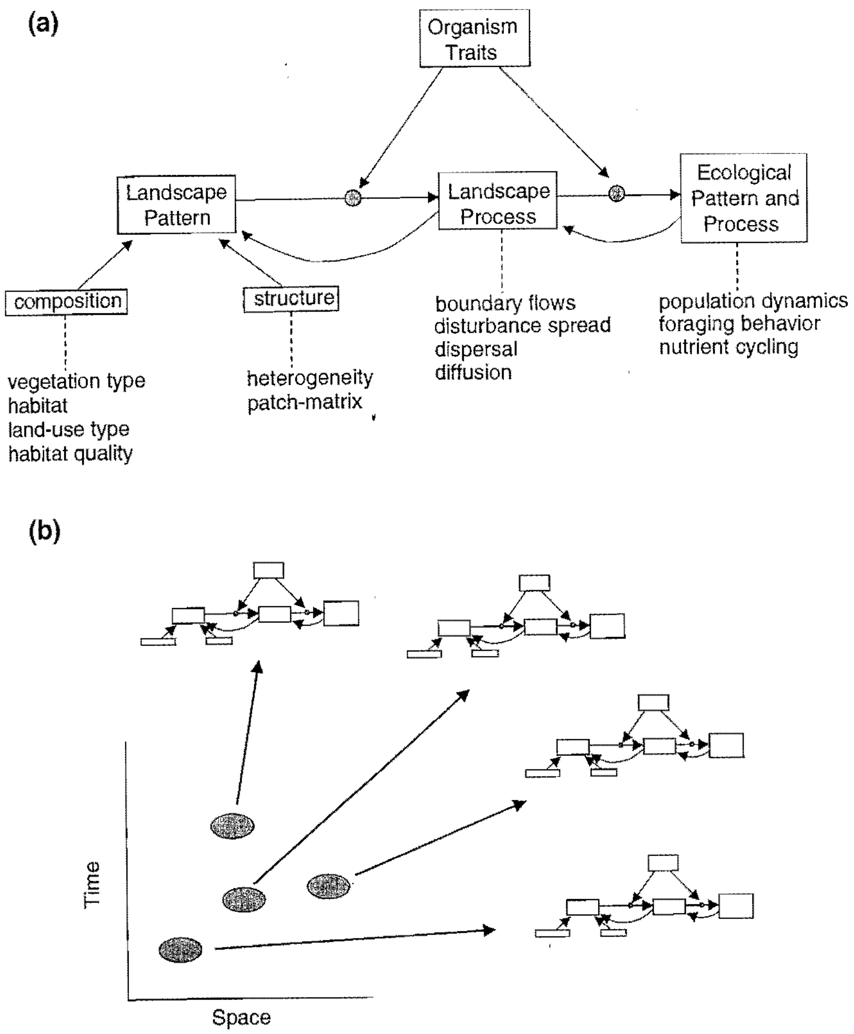

FIGURE 1.1. (a) Elements of a framework for thinking about landscape effects on ecological systems. The spatial pattern of a landscape is derived from its composition (the kinds of elements it contains) and its structure (how they are arranged in space). The spatial pattern of a landscape is translated into spatially dependent landscape processes as a consequence of the interplay between the landscape pattern and the ways in which different kinds of organisms respond to that pattern, which in turn is dictated by ecological, morphological, behavioral, and life-history traits of the organisms. The landscape pattern-process linkage, mediated again by the ecological traits of organisms, produces spatial dependencies in a variety of ecological phenomena. There are feedbacks among all of these relationships, but the most important are those from ecological patterns and processes that influence the nature of landscape processes, which is turn affect the underlying landscape patterns. (b) Because all of the components of the web of spatial interactions shown in (a) may change with changes in scale, the resulting ecological patterns and processes that we study and attempt to manage will probably differ among different space-time scaling domains (shaded ellipses).

responds to "habitat" may differ as well. At a more basic level, a classification approach can easily lead to a neglect of gradients in environmental factors by partitioning or "blocking" the variation that occurs along a gradient. This, in turn, may foster an avoidance of geostatistical analyses that explore the form of spatial correlation in ecological measures (see Fortin 1999). It is easy to regard maps or images as "truth" and to forget that any conclusions are contingent on the classification and boundary determination procedures used to produce the map (Monmonier 1996). Landscape ecologists would be well-advised to heed Austin's (1999) call for closer attention to environmental gradients and the form of species' response functions (what we used to call "niches").

Superficially, landscape pattern can be described in terms of patches, corridors, and the background matrix (Forman 1995). However, this categorization obscures some of the richness of detail that characterizes landscape mosaics, primarily because the "matrix" itself usually contains a variety of patches of different types and properties. In fact, a large array of features and measures can be derived from a map or image of a landscape (Table 1.1). Some of these measures, such as patch size or shape, nearest-neighbor distance, or perimeter:area ratio, portray features of particular patch types independently of their surroundings. Others, such as adjacency or contrast, deal explicitly with what lies across the boundaries of a given patch type. Still other measures—semivariance, lacunarity, fractal dimension, patch diversity, connectedness, or various indices of heterogeneity, for example—characterize features of the mosaic as a whole. Together with spatially referenced records or inventories of ecological variables of interest (e.g., population abundance, species diversity), these measures are the raw materials that are used to assess how landscapes affect ecological phenomena.

TABLE 1.1. Some measures of landscape structure. For convenience, the measures are separated into those that describe features of individual patches and those that express patterns of the entire landscape mosaic, although the distinction between the two categories is not always sharp. All of the patch-based measures can be characterized by a mean and a variance over the landscape as a whole, reflecting additional aspects of landscape structure. For additional details, see Haines-Young et al. (1993), Forman (1995), McGarigal and Marks (1995), Farina (1998), and Longley et al. (1999).

- Patch measures
  - Size
  - Shape
  - Orientation
  - Perimeter
  - Perimeter:Area ratio
  - Context (adjacency, contrast)
  - Distance (nearest neighbor, proximity)
  - Corridor width, length, shape, linkage (e.g., stream order)
- Mosaic measures
  - Patch number
  - Patch size frequency distribution
  - Patch diversity (richness, evenness, dominance, similarity)
  - Percent of landscape in a given patch type
  - Patch dispersion (contagion)
  - Edge density
  - Fractal dimension (edge, area)
  - Heterogeneity
  - Gaps (lacunarity)
  - Spatial correlation (semivariance, distance decay, anisotropy)
  - Connectedness (network, lattice properties)

1.3 Emerging Concepts of Landscape Ecology

The overarching principle of landscape ecology is that the spatial configuration of landscapes can have important effects on a wide variety of ecological processes. These, in turn, determine the ecological patterns that ecologists are so fond of documenting and theorizing about, and which form the foundation for most thinking in biological conservation. The particular spatial or locational arrangement of the various elements of a landscape produces ecological processes and patterns that are different from those that would emerge in a landscape with a different spatial configuration.

To relate the various quantitative measures of landscape structure and composition to ecological consequences, however, we need something more specific. I suggest that the following five concepts (I hesitate to call them "principles") can serve as a foundation for thinking about landscapes in an ecological or conservation context.

1.3.1 Landscape Elements Differ in Quality

The elements or patches in a landscape or map are distinguished from one another because they differ in some way. Traditionally, patch types are classified by differences in vegetation cover, soils, or geology, or forms of human land use, but other criteria may be used depending on the information available and one's objectives in describing or mapping a landscape. In the context of biological conservation, the focus is often on how organisms or populations are distributed in space, and the underlying premise is that the criteria used to portray the landscape relate in some way to "habitat" and, ultimately, to "habitat quality." Habitat quality, in turn, relates to the probabilities of survival and reproduction of individuals occupying a patch type—the patch-dependent fitness function (Wiens 1997). Differences in reproductive success or survival probability among patches (e.g., vegetation types) are clearly the norm for most (ultimately, all) species, but these components of fitness are difficult to document and indirect measures (especially local population density) are often used as surrogates of fitness-defined patch quality. Substantial problems are involved in using such surrogate measures, however (e.g., Van Horne 1983; Garshelis 2000), so although the notion of patch or habitat quality has clear conceptual appeal, operationally it remains difficult to implement.

Despite these difficulties, it is important to begin to think of landscapes in terms of patches or elements of differing quality rather than remaining content with descriptions of landscape patterns based on arbitrary criteria that have an unknown (but possibly remote) relationship to biological functions or processes. One cannot link spatial patterns to spatial processes using landscape measures that have little to do with process, regardless of how many people have used them in the past or how stunning they appear on a remote-sensing image or a GIS output. Understanding *why* organisms occur where they do or move as they do in a landscape requires a consideration of variations in patch quality. Of course, the quality of landscape elements is not a fixed attribute. Patch quality varies in time as resource levels change, predator or competitor abundances vary, or physiological stresses change. More germane here are the variations in patch quality that may result from the structural configuration of the mosaic in which the patches are embedded. These variations are the focus of the four remaining key concepts of landscape ecology.

1.3.2 Patch Boundaries Influence Ecological Dynamics Both Within and Among Patches

If the underlying premise of landscape ecology is true—if indeed the structural configuration of a landscape can affect both what goes on within as well as between landscape elements—then patch boundaries must play a key role in governing these effects. Boundaries are the "membranes" that enclose patches, and their permeability determines what flows into and out of patches, at what rates, and in what overall directions (Wiens 1992). Part of the concern about the effects of habitat fragmentation, for example, is related to boundary or edge effects. Fragmentation is usually accompanied by a reduction in patch size, increasing the perimeter:area ratio and reducing the proportion of the patch that contains interior or "core" habitat that is immune to edge effects. Many studies have documented reduced nesting success of forest birds close to the boundary of forest fragments, largely due to increased loss to predators crossing the boundary from adjacent patches in the landscape (e.g., Wilcove 1985; Andrén 1992). Apart from changes in predation risk associated with patch boundaries, how species within a patch respond to a boundary may affect their vulnerability to fragmentation. A species that will not cross a boundary into adjacent patch types will be much more likely to suffer reductions in population size and increased extinction probability than will one for which the boundary is more permeable, facilitating dispersal from the patch as well as movement into the patch from elsewhere in the landscape.

Often the boundaries themselves have important properties. Boundaries are often transition zones (ecotones) in microclimatic factors, such as wind speed or radiant energy inputs, and both primary and secondary production may be greater in the boundary zone. This phenomenon underlies the "ecological trap" idea, which hypothesizes that individuals may be attracted to establish breeding territories in boundary situations due to the greater abundance of food there, only to suffer increased predation risk from adjacent areas (Gates and Gysel 1978). The ecological importance of boundaries and ecotones is reflected in an extensive literature on their effects (e.g., Holland et al. 1991; Hansen and di Castri 1992; Gosz 1993).

1.3.3 Patch Context Is Important

Recognition of the importance of patch context is perhaps the essence of landscape ecology. One can assess how differences in patch quality or in movements across patch boundaries affect ecological systems without necessarily considering landscape structure, but it is impossible to address the effects of patch context without a landscape-ecology perspective. What is adjacent to a given patch can have powerful effects on what happens within that patch—its quality, the degree to which the patch boundary filters movements, and the like. For example, the magnitude of edge-related predation on songbird nests in forest patches may be strongly influenced by what lies across the forest boundary (e.g., Wilcove 1985; Andrén 1992). Such patch-context effects may extend to community features as well as to population processes. In desert systems, for example, riparian zones may serve as a source of emigrants for communities occupying adjacent landscape elements, but the extent of this influence (and thus the degree to which communities in the other landscape elements are affected by their adjacency to riparian areas) may differ for different landscape elements (e.g., lowland vs. upland; Szaro and Jakle 1985). Dan Janzen (1983) placed such landscape influences explicitly in a conservation context by observing that "no park is an island," that the surroundings of a park or nature reserve may have important effects on what goes on within the park. The potential of a park or reserve to attain conservation goals, such as preservation of an endangered species, may therefore be compromised by the nature of the surrounding landscape—the complement of predators, parasites, competitors, or disturbances that are available to cross the boundary into the "protected" area. This is why it is so important to know not only *what* a patch is, in terms of its size, boundary length, quality, and so on, but also *where* it is, in terms of its adjacency to different kinds of neighboring patches with different ecological properties.

1.3.4 Connectivity Is a Key Feature of Landscape Structure

Of all the features of landscape structure listed in Table 1.1, corridors and, less often, landscape connectedness have received the greatest attention from conservation biologists. The literature of biological conservation is rife with allusions to the importance of habitat corridors (see Bennett 1999). The usual theme is that *corridors*—more-or-less linear strips of habitat joining patches of similar habitat—may provide essential conduits that enhance movement of individuals between otherwise isolated patches. Corridors facilitate the "rescue effect" (Brown and Kodric-Brown 1977) and lessen the probability of local extinction of small populations in fragmented habitats. Contrary arguments have been raised, having to do primarily with the role that corridors may play in facilitating the spread of diseases or disturbances, or the movements of predators or species of concern (e.g., Rosenberg et al. 1997). Despite their intuitive and logical appeal, evidence for the efficacy of corridors is nowhere near as compelling as the enthusiasm with which corridors have been embraced as a conservation and management tool would seem to suggest (Hobbs 1992; Bennett 1999).

Beyond any debates about the value of corridors in conservation, a focus on corridors tends to perpetuate a simplistic patch-matrix view of landscapes and to obscure the true functional connectivity of landscapes. *Connectivity* (or *connectedness*) is an aggregate property of the structural configuration of elements in a landscape mosaic, their relative viscosities to movements, and the relative permeabilities of their boundaries (Taylor et al. 1993; Wiens 1995; Tischendorf and Fahrig 2000). The probability that an individual will move from one place in a landscape to another (which is what matters in thinking about such things as metapopulation dynamics or fragmentation effects) is therefore determined by the factors underlying the previous three key landscape ecology concepts—patch quality, boundary effects, and patch context—*and* by how different kinds of organisms respond to these features of landscapes. In the Western Australian wheatbelt, for example, Blue-breasted Fairy-wrens (*Malurus pulcherrimus*) are restricted to scattered remnants of native vegetation. Dispersal among such patches is inhibited by gaps in vegetation greater than roughly 60 m (Brooker et al. 1999), so linkages among patches to form dispersal neighborboods are determined largely by the configuration of well-defined vegetated corridors along roadways or fencelines (L. Brooker and M. Brooker, unpublished manuscript). Other species occupying the same habitats, such as Singing Honeyeaters (*Lichenostomus virescens*), are less reluctant to move into and through other patch types, and for them the connectivity of the landscape is much greater (Merriam and Saunders 1993). Dispersal is a key population process, yet the probability that individuals will successfully disperse from some origin (e.g., a birthplace) to some destination (e.g., breeding habitat) involves much more than simple linear diffusion or distance-decay functions. The composition and physical configuration of the landscape can have a profound influence on dispersal pathways (Wiens 2001), with the result that different landscape structures can produce quite different demographics.

1.3.5 Spatial Patterns and Processes Are Scale-Dependent

Perhaps because of the close ties of landscape ecology with geography and cartography, and thus with maps, considerations of scale have been a central focus since its beginnings. Indeed, the emergence of landscape ecology as a discipline has done much to increase the awareness of ecologists of all sorts of the importance of scale. This recognition of scale dependency and scaling relationships runs counter to the reductionist theme that has recently dominated ecology, which has emphasized studies and experiments at fine spatial and temporal scales and simple mathematical models that ignore scale, and often space as well (Wiens 1995). "Scale" has been called a "nonreductionist unifying concept in ecology" (Peterson and Parker 1998). Despite this, there is yet no formal "theory of scale" in landscape ecology (Meentemeyer and Box 1987; Wiens 1989a), and ecologists use "scale" in many ways (see the long table in Peterson and Parker 1998). I follow O'Neill and King (1998) in insisting that scale can only refer to dimensions in space and time.

Part of the problem is that as these dimensions change, both patterns and processes change, often in complex ways. The physical processes or anthropogenic factors that affect landscape structure, for example, differ at different spatial scales (e.g., Krummel et al. 1987; Ludwig et al. 2000), and different organisms perceive and respond to landscape structure at different scales (Wiens et al. 1993; Haila 1999; Mac Nally 1999). More often than not, the changes in relationships with changes in scale are strongly nonlinear. The thresholds in scale dependencies serve to define *scaling domains,* within which scaling relationships are consistent and extrapolation among scales is possible, but between which the rules change and extrapolation is difficult or impossible (O'Neill 1979; Wiens 1989a). The linkages between landscape pattern, landscape processes, and ecological consequences are therefore likely to be played out in different ways at different scales (Figure 1.1b). As a consequence, virtually all ecological patterns and processes are sensitive to scale.

When we observe these ecological phenomena, we do so through a window whose size is set by the minimum scale of resolution (the *grain*) and the overall scope (the *extent*) of our observations (e.g., the size of individual sampling units and of the area in which they are distributed, respectively). Changing either the grain or the extent changes the observation scale and, thus, the subset of ecological patterns, processes, and relationships that we perceive. It is no wonder that studies of the same phenomena conducted at different scales usually yield different results. In a conservation context, the problem is compounded when an arbitrary scale of management is imposed on ecological systems that are in fact operating at different scales (Wiens et al. In press). As conservation efforts shift from a focus on single species of concern to multiple species, ecosystems, or landscapes (Franklin 1993), the difficulties of dealing with scaling effects will be exacerbated, as both the ways in which landscape structure is affected by human land use or management actions and the ways in which the varied components of the system respond to landscape structure change with changes in scale.

1.4 Integrating Landscape Ecology With Biological Conservation

Changing land use is one of the major forces leading to the changes in population sizes, species distributions, ecosystem functions, or biodiversity that concern conservation biologists. Land use has these effects by altering the features and functions of landscapes that are embodied in the five concepts just described, so there should be little doubt about the relevance of these concepts, and of landscape ecology, to conservation issues. Apart from the details of implementing a landscape approach in biological conservation (e.g., which variables to map and measure, at which scales?), however, several broader issues should be addressed.

1.4.1 *Is Landscape Ecology Landlocked?*

Conservation, of course, involves more than land. Historically, however, landscape ecology has dealt almost entirely with land—with the components of terrestrial ecosystems and human land use. To be sure, lakes, streams, and rivers have often been included in analyses of landscape patterns, but usually as only one of many elements of the landscape mosaic (e.g., as "water" in remotely sensed images). Ecosystem ecologists have made liberal use of watersheds to integrate land and water dynamics within a defined area, but the spatial patterns within a watershed or exchanges across its boundaries have received much less attention. Stream management has often incorporated consideration of the adjacent riparian vegetation as a buffer zone to maintain stream integrity, but the landscape beyond the bordering riparian strip has often been considered only as a source of water, nutrients, or pollutants, with no explicit spatial structure of its own (but see Malanson 1993; Ward 1998; Wear et al. 1998).

Despite appearances, the central concepts of landscape ecology have been an implicit part of aquatic ecology for some time. Oceanographers, for example, have been dealing with scaling effects for decades (e.g., Steele 1978, 1989), and Hutchinson (1961) explained the paradox of high species diversity among planktonic organisms in terms of the complex, three-dimensional spatial heterogeneity of oceans. Aquatic ecologists have traditionally viewed streams as a mosaic of riffles, pools, and stream segments with high physical connectivity (e.g., Poff and Ward 1990; Robson and Chester 1999). Concepts of patchiness and patch dynamics (e.g., Kling et al. 2000; Palmer et al. 2000; Riera et al. 2000) and of scale (e.g., Poff 1996; Cooper et al. 1998; Lodge et al. 1998) have become central to how aquatic ecologists think about streams, rivers, and lakes. Spatial structure and dynamics may be more difficult to document and measure by remote sensing and GIS in aquatic systems than they are on land, but this does not mean that the interplay of landscape patterns and processes shown in Figure 1.1a is any less important. If landscape ecology is indeed the study of spatial patterns and processes, then it is just as relevant to water as it is to land. The "land" in "landscape ecology" should not be taken too literally.

1.4.2 *Does Landscape Ecology Offer More Than Pretty Pictures?*

To many people, the power of landscape ecology lies in its maps and images, and in the analyses and modeling that can be done using such pictures. Technological advances have led to rapid increases in the sophistication of such descriptions of landscape patterns. Remote sensing can now supply vast sets of spatial data, and GIS is a magnificent tool for integrating such information and depicting both real and synthetic landscape patterns. Our ability to construct spatially explicit simulation models that track the locations and responses of numerous individuals and their interactions with the landscape is limited more by our skill in structuring logical models and specifying reasonable parameter values than by computational capacity or speed. The value of spatial statistics is now recognized by many ecologists as well as statisticians, and the array of geostatistical tools and the software to enhance their use are expanding rapidly. Both GIS and spatial models are being used in innovative ways to explore the scaling properties of landscape patterns.

Biological conservation requires a rigorous scientific foundation, which landscape ecology should seek to provide. Certainly the quantitative rigor of landscape studies has been greatly enhanced by tools such as remote sensing, GIS, spatial modeling, and spatial statistics. Landscape ecologists also have had some success in approaching landscape problems experimentally, either by designing real experiments using fine-scale experimental model systems (EMS), or by opportunistically studying landscape alterations such as grazing or timber harvesting as quasi-experiments. By and large, however, the approaches we have come to associate with scientific rigor in ecology as a whole—experiments, an emphasis on mechanisms, explicit hypothesis testing, mathematical modeling, and well-developed, predictive theory—are generally not well-suited to dealing with landscapes. The array of possible spatial configurations of landscapes is too great, the range of relevant scales too broad, and the diversity of responses to landscape patterns and processes too large to mesh well with traditional reductionist approaches. It is the classic "middle-number" conundrum of ecology (Allen and Hoekstra 1990; O'Neill and King 1998; Lawton 1999), in which the phenomena studied are not small or simple enough so that one can deal with individual components, nor large enough that one can examine the statistical properties of the systems without worrying about individual details (as in the gas laws of physics). Rather, ecological systems often fall between these extremes: there are too many individual components, with too many complex interactions, to deal with the individuals, yet the individual details affect the dynamics of the system as a whole, so general statistical properties yield incomplete pictures of what is going on. In the case of landscapes, the problem is amplified by spatial variation and interdependencies, scale dependencies, and thresholds.

The difficulties seem especially great when it comes to developing a strong theoretical foundation for landscape ecology (Wiens 1995). Landscape ecologists have developed a lot of verbal theory, which casts ideas in prose rather than in mathematics. Verbal theory is exemplified by the concepts discussed above. However, such theory, being verbal, lacks the rigor and precision we have come to expect of "real" (i.e., mathematical) theory. As a result, the capacity of landscape ecology to provide a theoretical foundation for conservation actions, or even to offer conceptual insights that can be used to generalize among conservation problems, seems limited. Consider an example. Metapopulation theory has become an important element in assessing conservation strategies for threatened or endangered species and in predicting the consequences of habitat fragmentation (see, e.g., the papers in McCullough 1996). It calls explicit attention to the demographic and genetic consequences of the spatial subdivision of populations, and it has been an important contributing factor to the increased focus on corridors in conservation design (Bennett 1999). Yet most metapopulation theory, and virtually all of its application, uses a simple patch-matrix or patch-matrix-corridor characterization of spatial pattern (Hanski 1999). Building more spatial texture and realism into models (or management protocols) diminishes their generality. It is not simply that the core concepts of landscape ecology (its verbal theories) are not recognized, although too often they are not. Rather, the kinds of spatial variance and scaling phenomena they emphasize do not fit well into traditional (i.e., mathematical) ways of theorizing.

1.4.3 Is Landscape Ecology Too Complex?

Landscape ecology has helped to crystalize the ongoing paradigm shift in ecology, from one portraying ecological systems as homogeneous, stable, closed, and scale-insensitive to a view emphasizing their spatial and temporal variability, openness, and scale dependence (Pickett et al. 1992; Wiens 1995). One consequence of this paradigm shift has been a flowering of complexity in time and space. Such complexity, of course, is the nemesis of theory, which thrives on simplification. So, although much of the recent history of ecology has emphasized understanding phenomena by generalization and simplification (i.e., through theory), embracing complexity seems to be the forte of landscape ecology. The devil, as they say, is in the details.

Certainly landscapes *are* complex. By adding spatial effects to the nonspatial way we have traditionally viewed ecological phenomena, contingent effects are increased factorially. Scale, of course, complicates things even more. It is reasonable to ask how much of this detail is really critical, how often we must be spatially explicit, or how much scale really matters. Must the answers to every conservation problem be sought in the idiosyncratic details of each situation? Can some (or perhaps most) of the details of landscape structure be ignored in the interests of generating coarse, but workable, solutions to the problems? An analogy with population dynamics theory and population management may be useful here. Populations, of course, are full of complexity—individual variation in genetics, age, nutritional state, behavior, experience, mating success, and so on. Yet population dynamics models that ignore most of this variation have been the foundation of population management for decades. More often than not, the simplifications have not mattered (or so we think), although there have been some notable failures (e.g., fisheries management; Botkin 1990). Can we somehow simplify our treatment of spatial patterns and processes? Do we need to put much detail into the boxes of Figure 1.1a?

The answer is that we simply don't know. In the history of dealing with population dynamics, simple mathematical theory developed in concert with, or in advance of, empirical studies. As a consequence, our understanding of population processes has largely been channeled in the directions dictated by theory. Because landscape ecology so far lacks such cohesive theory, the empirical findings are mainly responsible for how we view spatial effects and scaling. By and large, these studies consistently show that space and scale *are* important, often in dramatic ways. If our assessment of the habitat associations of a bird species, for example, can change from strongly positive to strongly negative with a change in the scale of analysis (e.g., Wiens 1989b), or if the net reproductive output of a local population changes from positive to negative with a change in patch context (e.g., Pulliam 1988), what does this portend for the success of conservation practices that fail to consider scale or landscape structure? It seems to me that the default position must be that the various landscape effects I have discussed here are likely to be important unless there are good reasons to think otherwise. As Hanski (1999:264) has noted, "the really important issue is whether spatial dynamics are considered at all in landscape management and conservation."

1.5 Concluding Comments

As it has emerged as a discipline in its own right, biological conservation has looked to ecology for general laws to guide conservation actions. If we are to believe John Lawton (1999), such laws will be most likely to emerge at the reductionist (i.e., population) and expansionist (i.e., macroecological) ends of the spectrum. Lawton specifically argues that because it is so plagued by the contingencies of middle-number systems, community ecology "is a mess" and should largely be abandoned. By adding the contingencies produced by spatial patterns, spatial processes, and their interactions (Figure 1.1a), not to mention scale (Figure 1.1b), landscape ecology must be an even greater mess. Perhaps all of this talk about patches, boundaries, connectivity, scale, and spatial processes should be ignored in the interests of getting on with the business of developing general laws that can help us solve conservation problems. Before taking salvation in Lawton's view, however, it might be good to consider the words of E. O. Wilson (2000). Writing explicitly in the context of conservation issues, Wilson suggests that community ecology (and, by inference, landscape ecology) "is about to emerge as one of the most significant intellectual frontiers of the twenty-first century." The contributions to this volume should help you decide who is right.

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